Functional traits complicate the picture of temporal biodiversity change in bird and mammal communities

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Abstract

Aim: Despite unprecedented environmental change due to anthropogenic pressure, recent work has found increasing species turnover but no overall trend in species diversity through time at the local scale. Functional diversity provides a potentially powerful alternative approach for understanding community composition by linking shifts in species identity to mechanisms of ecosystem processes. Here we present the first multi-taxa, multi-system analysis of functional change through time.

Location: Global, with a North American focus

Time period: 1923-2014

Major taxa studied: Mammals, Birds

Methods: We paired thousands of bird and mammal assemblage time series from the BioTIME database with existing trait data representative of a species' functional role to reconstruct time series of functional diversity metrics. Using generalized linear mixed models, we estimated general trends in those metrics and trends for individual studies.

Results: We found no overall trend in any functional diversity metric, despite data replicating species-based patterns of constant richness with increasing turnover. The lack of trend held even after correcting for changes in species richness. At the study-level, there were also a substantial number of time series exhibiting no species or functional change, however most studies showed a shift in a species or functional metric.

Main Conclusions: General trends indicate that on the aggregate one type of functional shift is not more prevalant than the other across many taxa, biomes, and realms. At the study-level, we identified four prevailing scenarios of species and functional change, which showed links to the duration of the observation window. With no one prevailing scenario of change, it will be critical to link change scenarios to drivers of change, particularly to identify communities with capacity to resist drivers from those not experiencing substantial pressure from a driver.

1 Introduction

Ecological communities are experiencing unprecedented change as a result of anthropogenic pressures such as climate change, land use change, and invasive species. Impacts of these pressures are well documented at a global scale by an accelerating global extinction rate (1), and fundamental changes in some of the most well-studied systems (e.g. coral bleaching, 2). At the local scale however, species diversity tells a different story. Recent syntheses of local trends in biodiversity over time have found no net change in local species diversity despite ongoing turnover (3–6) and evidence of significant shifts in community composition

underlying consistent species richness (7–9). While communities are clearly changing, our most common species-based approaches do not fully capture the nature of that change.

The meaning of general trends derived from limited data, and their relevance for conservation, is a topic of on going debate. Global analyses have been heavily criticized for geographic biases, lack of data in the most heavily impacted areas, and exclusion of individual studies' ecological context (10–12). Many of these criticisms reflect limitations of ecological data on the whole, leading to a call for additional data not only to fill geographic and temporal gaps, but to flesh out key characteristics of communities (13, 14).

Functional diversity offers a potentially powerful addition to species-based approaches for detecting and describing community change by providing a mechanistic link between species' response to environmental change (*response traits*) and the processes they perform (*effect traits*) (15–17). By describing the functional trait space, functional diversity metrics capture the disproportionate impact of losses or gains of functionally unique species. Functional diversity metrics may therefore illuminate joint responses from functionally similar species or communities undetectible by looking at species identity alone.

The expectation for functional change across communities is not obvious from past work, and may or may not follow taxonomic trends (13). While functional loss is frequently cited as one of the most pressing concerns of the anthropocene (18–20), functional diversity may be maintained even when species are lost from a community (21, 22). Forecasts of functional loss range from negligible (23) to dire (24, 25). And while some observed trends show significant functional loss (26) others document no loss even in some of the most heavily impacted communities (27–29). On paleoecological time scales, functional composition shows mixed responses to environmental change and extinction events (30, 31), with significant impacts of species extinctions on functional diversity in some taxa and not others (32). For some time periods, functional structure appears to be maintained for substantial portions of geological time (33). Contemporary, broad-scale examinations of functional change are limited to only a few taxa-focused studies, but show for example functional richness increases for both North American birds [@barnagaud2017; @jarzyna2016] and ray-finned fishes, sharks, and rays (34).

Here we leverage ongoing efforts to assemble functional trait data and recent computational advances to perform the first multi-taxa, multi-realm assessment of functional diversity change through time. We focus on mammal and bird species as a significant subset of the world's biodiversity heavily impacted by anthropogenic change. While examining trends in plants, invertebrates, and other vertebrate species is of equal interest, trait data for those taxa raise additional challenges such as limited and biased species coverage (35), a lack of accepted species-level means, and differences in the types of traits collected. To ensure comparability across taxa in trait type and data quality we therefore focus on mammals and birds. Traits were intentionally selected to be representative of a species' Eltonian niche, thereby summarizing the functional role they play in the community (36). An initial assessment of amphibian trends is included in the supplement, but excluded from general trend assessment here due to limited geographic coverage.

We assess thousands of mammal and bird functional diversity time series to determine whether or not the addition of functional trait data gives a clarifying picture of biodiversity change across communities. Rather than testing specific hypotheses of change we present a few areas of change consensus across communities, and even more scenarios where the relationship between functional and species change are unexplained and warrant further theoretical and experimental examination. We present results at three different levels: general trends across communities, trends for communities with similar characteristics (taxa, biome, realm, protection status), and trends for individual studies.

2 Material and Methods

2.1 Data

We obtained mammal and bird time series from the BioTIME database, a global repository of high-quality assemblage time series. All studies included in the database follow consistent sampling protocols and represent full assemblages rather than populations of single species (31). All time series include abundance of observed species. Following best practices for the database (37), studies with multiple sample locations were split into individual time series following a standardized spatial scale. Scale was set by a global grid with cell size determined based on the sample extent of studies with only a single location (see 31 for details on how sample extents were defined), with the area of each cell set to one standard deviation away from the mean of the single extent locations. All samples from a study within a single cell were considered to be a single time series, and species abundances were combined for all samples.

We used trait data from the Elton Trait Database, which consists of species-level means for traits that represent species' multifaceted role in the community (36). Traits include: body mass, diet, active diel period, nocturnality, forest foraging strata, pelagic use. Multiple traits (i.e. diet, foraging strata, activity seasonality, active diel period) were broken down into percentage or binary use for each level.

In order to ensure taxonomic consistency across datasets, BioTIME species were paired with trait data based on their species identifier from the Integrated Taxonomic Information System database (retrieved 09-15-2020 from the on-line database, `https://doi.org/10.5066/F7KH0KBK`), obtained through the `taxadb` R package (38, 39). If more than one species in the assemblage data resolved to the same identifier, observations were considered the same species. For trait data, traits for all species of the same identifier were averaged. Only studies for which at least 75% of species had trait data were included. In order to have a sufficient number of species to calculate functional diversity metrics, years with fewer than 5 species observed were also excluded. Sensitivity analyses were conducted for the trait coverage threshold and the duration of included time series.

Many studies had a variable number of samples within years. To account for this inconsistency in sampling effort we used sample-based rarefaction by bootstrap resampling within years for each time series based on the smallest number of samples in a year for that time series.

Our final dataset included 2,432 time series from 50 studies in 21 countries and 12 biomes and 6 different traits (Fig 1). Data came from both terrestrial and marine realms and five climates (Global, Polar/Temperate, Temperate, Temperate/Tropical, Tropical). The earliest sample was in 1923 and the most recent was in 2014. While it is not possible with this data to directly assess the level of human impact occurring for each study, we include binary protection status as a coarse indicator of impact level. However, protected areas were almost exclusively from temperate terrestrial studies (with one tropical study), so results are confounded by multiple other study characteristics. For a full breakdown of studies and their characteristics, see the supplement. Our final dataset reflects many of the data biases that make global synthesis work challenging, including geographic bias, a bias away from areas currently under the greatest threat, and a bias towards shorter time series. We address these shortcomings and their potential impact on our results in the discussion.

2.2 Diversity Metrics

We calculated yearly metrics of functional and species diversity for each time series. Species-based metrics include species richness (S) and Jaccard similarity (J) as a measure of turnover. Jaccard similarity was calculated relative to the first observed year for a time series. A negative trend in J would therefore indicate increasing turnover. We did not impose a correction for unobserved species as non-parametric estimators do not assign species identities to corrected richness values, and therefore could not be propagated to the functional diversity metrics.

Functional diversity metrics were calculated using the *dbFD* function from the *FD* R package (40). Here we report functional richness (*FRic*), functional evenness (*FEve*), and functional divergence (*FDiv*) which together describe three complementary characteristics of the functional space (41, 42). *FRic* assesses the volume of the trait space occupied by species in the community, with higher values indicating communities with species of more extreme trait values. *FEve* describes how species are distributed across the trait space and how abundance is distributed across species. Higher values of *FEve* indicate more even spacing of species in the trait space and individuals across species. *FDiv* measures the degree to which species and their abundances maximize differences in the functional space. Higher values of *FDiv* therefore correspond to communities where many highly abundant species are on the edges of the trait space. We also calculated the community-weighted mean (*CWM*) of included traits to examine shifts in the distribution of each trait. Hereafter we refer to results for functional diversity metrics (FRic, FEve, FDiv) and composition metrics (trait CWM's).

All available trait data for each study were included in functional diversity calculations with the exception of traits that were the same value for all observed species in the study. For variables with multiple levels each level was included as a separate trait axis. Continuous traits were z-score scaled to give each trait equal weight in the trait space (43, 44). Before calculating diversity metrics, dbFD reduces the dimensionality of the trait space by performing PCoA. We limited the number of included PCoA axes to the maximum number of traits that fulfills the criteria $s >= 2^t$, where s is the number of species and t is the number of traits. This restriction allows for enough axes to capture the trait space while maintaining computational feasibility (45). Metrics incorporated weighting based on species abundance.
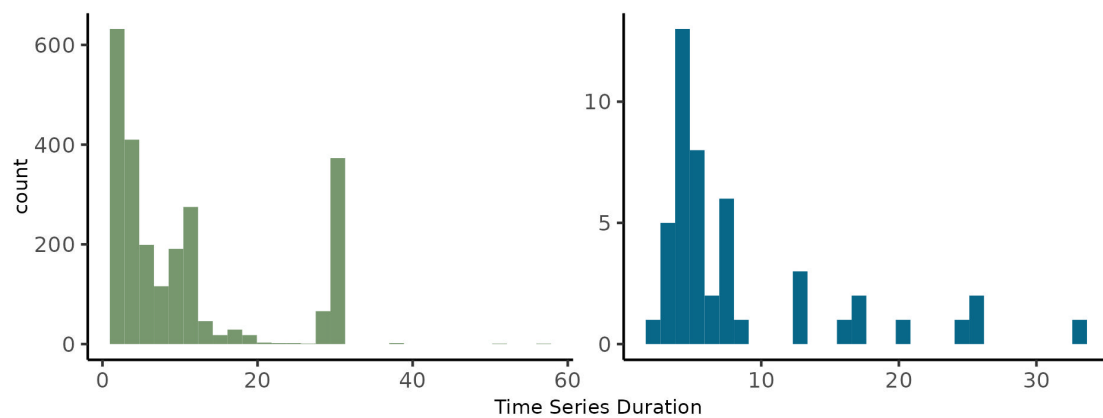
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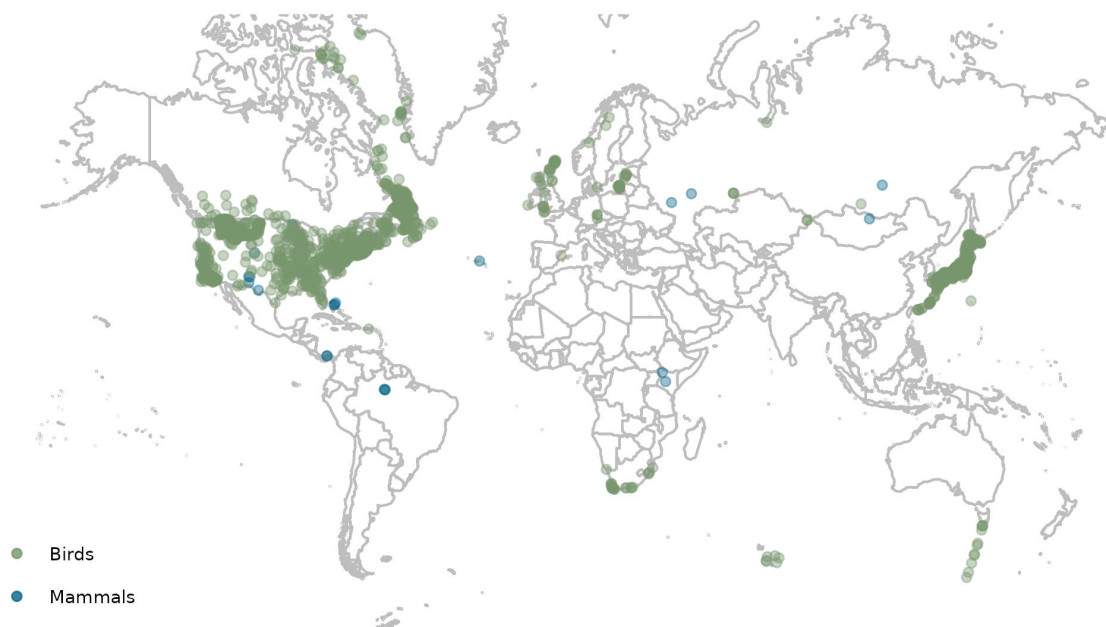
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Figure 1: A) Map of time series locations with points colored by taxa, and B) histograms of time series duration broken down by taxa.

2.3 Null Models

To assess functional change independent of species richness we calculated the standardized effect size (SES) for each of the three functional diversity metrics (*FRic*, *FEve*, *FDiv*) from null estimates (46). Null model corrections allow us to assess the degree to which the observed functional diversity metric deviates from the value expected by chance in a randomly assembled community. Null estimates were calculated for each rarefied sample by randomly sampling species from the species pool for each year and randomly assigning observed abundances to species. ' Species pools were unique for each time series and included all species observed over the course of sampling, therefore accounting for geographic restrictions in species availability. This process was repeated 500 times to get an estimate and standard deviation of the null expectation for the metric for each rarefaction sample for that time series. We used these values to calculate SES using the following formula: $SES = [F_{obs} - mean_{(F_{null})}]/SD_{(F_{null})}$. We then calculated the median SES estimate for each metric from all the rarefaction samples for a time series. SES estimates can be interpreted as how much of the functional characteristic (richness, evenness, divergence) was observed beyond what was expected by chance for a community of that species richness.

2.4 Analysis

We estimated general trends across bird and mammals communities for each diversity metric using a linear mixed effects model with a random slope and intercept for each study and each time series nested within the study. We fit 18 individual *CWM* models. All time series with data for a given trait were included in the corresponding *CWM* model. We estimated study level trends using individual linear models. For studies with more than one times series we fit a random slope and intercept for time series. Some study-level models could not be fit for five studies for at least one metric due to data limitations, but those studies were still included in the general models. They represented 12 of 1350 study-level models fit for each metric. For further details see the supplement. Where appropriate, response variables were *log* or $log(x + 1)$ transformed to better fit model assumptions of residual normality.

To test for trends within and between different levels of taxa, biome, realm, and protection status we fit separate models with each of those factors added as a predictor interacting with time to the original model structure. We estimated within-level slopes and calculated between-level contrasts using the *emmeans* package (v1.8.2, 47). We assessed the impact of time series duration and start year on study-level trends using linear models with duration and start year as predictors. All models in our analysis were fit using the *lme4* (v1.1-30) package in R (v4.2.3) and p-values were calculated by Satterthwaite's degrees of freedom method using the *lmerTest* (v3.1-3) package with a significance level of $\alpha = 0.05$ (48–50).

3 Results

We found no significant overall trend in species richness or functional diversity metrics (observed or corrected) (Fig 2). We did find a significant overall decrease in Jaccard similarity, indicating accumulating changes in species composition. Non-significant overall trends indicate that although some studies experience increasing or decreasing trends, the average trend across studies was plausibly 0 (Table **??**). Within-group trends for different taxa, biomes, realms, or protection statuses were also non-significant for richness and functional diversity metrics, with the exception of a significantly increasing trend for functional evenness of global studies (characterized by having samples on multiple continents), and a significantly decreasing functional richness slope for temperate/tropical studies and mammal studies. However, trends were not exhibited for the corrected metric indicating that differences in functional diversity metrics were largely due to changes in species richness. Further, with only two global studies, the trend should not be considered truly general. The general trends for *CWM* models were similarly not significant, with a significant positive trend for only percentage of fish in diet composition.

We did find significant differences between taxa, realms, and climate for Jaccard similarity and some of the *CWM's*. For example, while Jaccard similarity was decreasing in the general trend and there were significant within group slopes for Mammals, Birds, and Terrestrial communities, there was no significant slope for the marine realm, indicating that the general trend is mostly driven by turnover in terrestrial communities. We also found a significant decrease in Jaccard similarity in unprotected areas only, with no trend for protected areas. For bird communities, we also found within group trends and between group differences for trends in foraging behavior. We found a significant increasing trend in utilization of the canopy in Tropical communities that was significantly different from the trends for Polar/Temperate and Temperate communities. There was a significant decrease in utilization of the understory for Terrestrial communities and significant increase in
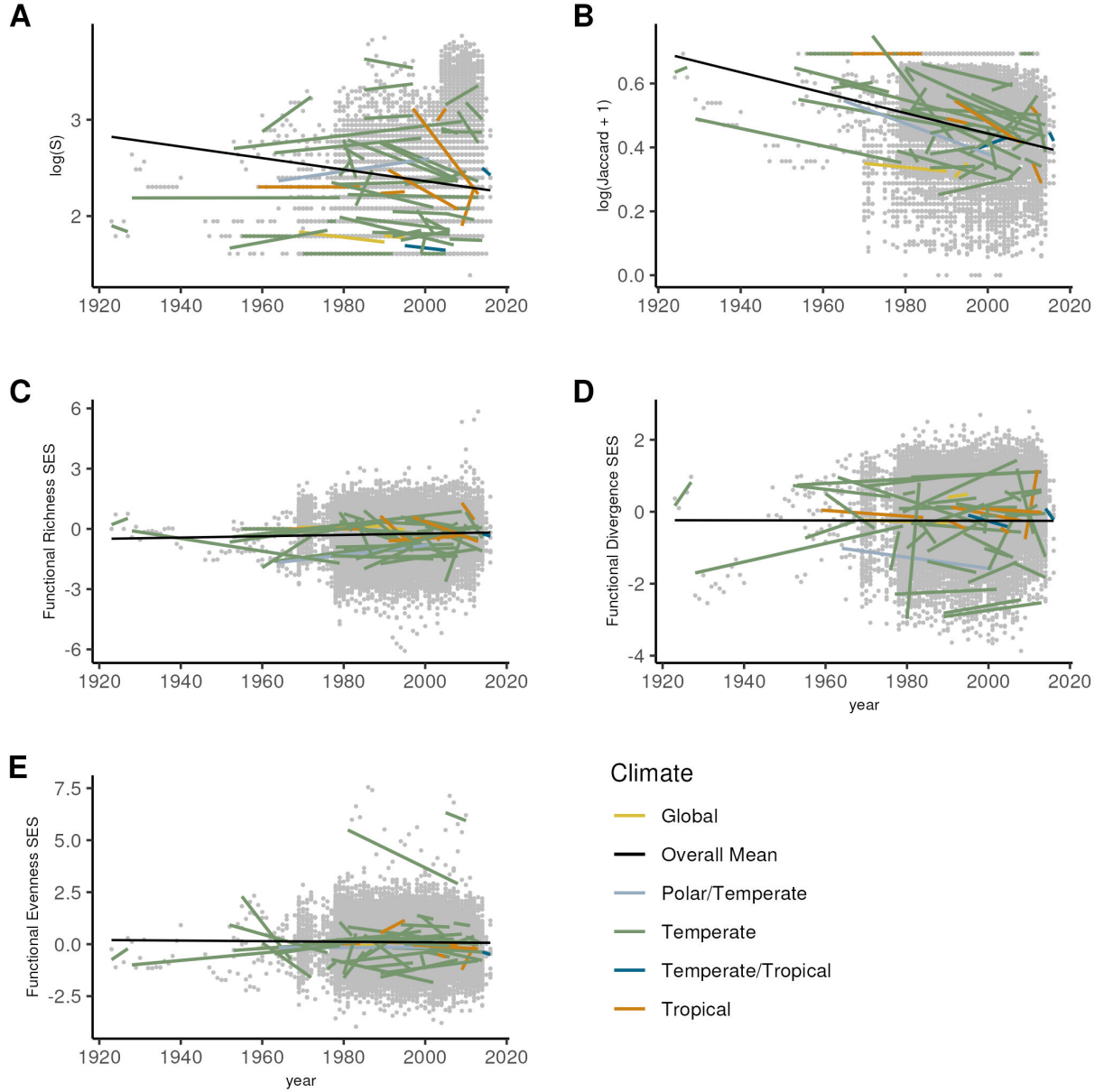
Figure 2: Plots of time series-level trends with line color corresponding to climatic region, with data points in grey and the overall metric mean in black for A) log species richness, B) Jaccard similarity, C) Functional Richness SES, D) Functional Divergence SES, and E) Functional Evenness SES

foraging below the water surface for global studies (but see the previous limitations of Global data). There was also a significant positive slope for *CWM* body mass for the single Temperate/Tropical study (with three time series) which were marine mammal communities.

We found significant dietary shifts across communities, with a significant increase in fruit consumption in Terrestrial communities and a significant decrease in nectar consumption in Tropical communities, a trend significantly different than that for Terrestrial communities. There was a significant increase in seed consumption in bird species, which was significantly different from the trend for Mammal communities. There was a significant increase in fish consumption for the two Global studies. Vertebrate consumption significantly decreased for Marine studies and for studies of Global and Tropical communities. There was also a significant increase in fish and fruit consumption for unprotected areas, but not protected.

At the study level, 15 of 50 studies exhibited a significant trend in species richness and 11 exhibited significant turnover. For observed functional metrics, 25 of 50 studies exhibited a trend in a least one metric, and 15 of 50 studies exhibited a significant trend for at least one corrected metric (Table **??**). In general, there were more significant trends for uncorrected metrics, with some disappearing after correction, indicating that those trends were likely due to changes in the number of species. Hypothesis testing for study-level trends is likely affected by multiple testing issues and some trends identified as significant are therefore potentially spurious. Rather than interpreting changes in specific studies, we present these results as a general picture of the kinds of trends experienced by communities.

Study-level slopes for functional diversity metrics were significantly related to start year of the time series for Jaccard similarity and functional evenness, both of which had significantly more negative slopes with more recent start year. No functional diversity metrics were significantly related to the start year of the time series.

We assessed the sensitivity of general trend results to major data processing decision by rerunning models with increasingly conservative subsets of the data. After excluding time series with less than two, three, and four year durations, we found that the general trend for increase in CWM aerial foraging disappeared, but two other trends in CWM's appeared. After excluding time series two years long, a general trend appeared for increased CWM use of the forest canopy, and decreased CWM of seed consumption. These two trends remained as increasingly shorter time series were excluded suggesting the increase in aerial foraging was an erroneous finding while the other two trends were more robust. Percentage of species in a community with trait data did not appear to have an affect on general trend results, as general trends were unchanged with increasing cut offs for percentage of species with trait data. A complete list of models run in the sensitivity analysis and their results can be found in the supplement.

4   Discussion

Our study represents the largest broad-scale multi-taxa assessment of functional change through time to date, giving a first look at aggregate and local trends in functional diversity in mammal and bird communities. Our results show that the addition of functional traits illuminates a few consistent functional trends across communities, but largely complicates rather that clarifies the story of biodiversity change. While the characteristics of species clearly matter, instead of unifying the nature of communities' change, they more often distinguish them. In general, we found a few areas of consensus for models where communities were aggregated (general trends, trends by taxa, biome, realm, protection status), and vast heterogeneity for study-level models.

4.0.1   Evidence of consensus

The most stark area of consensus was the lack of general trend aggregating across communities. We did not detect an overall trend in any functional diversity metrics. As with previous species-based syntheses, we also found no overall trend in species richness accompanied by increasing turnover through time (31), indicating that non-significant trends in functional metrics are consistent with similar well-documented species derived trends. We found no trend in functional change for almost all realms, biomes, and taxonomic groups. The one exception was a consensus trend indicating functional richness loss for mammal studies. These results are consistent with multiple studies linking anthropogenic drivers to loss of functional diversity in mammal communities (51–53).

Despite a lack of general trends in functional diversity metrics, we did find evidence of compositional shifts in the trait space with multiple `significant` trends in *CWM*'s for studies coming from the same taxa, realms, climates, or protection statuses, `indicating areas of consensus change across communities`.

Some of those trends are consistent with existing work in those contexts. For example, the decrease in insect consumption for tropical communities reflects well documented declines in tropical insectivorous birds (54). Reduction in utilization of understory foraging for terrestrial communities could be the result of disturbance like human recreation or increased predation from introduced species. Other shifts in diet for both Birds and Mammals, including increasing fruit, seed, and vertebrate consumption and decreasing seed consumption in some climates point to important areas for further exploration.

4.0.2 Study heterogeneity

At the study-level, our results run contrary to our hope for a clearer picture of biodiversity change through a functional lens. The lack of general trend in functional diversity metrics belies a huge range of positive and negative trends at the study-level. In order to simplify discussion, we will talk about the implications for ecosystem process and vulnerability for communities grouped by their concurrent change in functional diversity metrics, species richness and turnover split into positive, negative or no trend. While there are over 150 possible combinations of change direction (or no change) in the 5 metrics, we discuss here the six scenarios that occurred in more than one study: no change, species loss or gain only, loss of functional evenness, richness loss with species turnover, and increase in species and functional richness accompanied by significant turnover. We focus on these scenarios to combat potential spurious results due to multiple testing, as it is unlikely all observations of the same scenario are due to false positives. We include a break down of the number of studies in each scenario to illustrate relative number of studies in each group, but emphasize that the absolute number is likely impacted by multiple testing.

The majority group of studies exhibited no trend in any species or functional diversity metric. Contrary to the expectation due to anthropogenic and global change stressors, these communities do not show significant changes over the course of the observation window. Studies in this group span the distribution of study durations excluding only the very longest running studies, with the longest no change time series lasting 23 years. They also included both bird and mammal studies and only four were located in protected areas, indicating that the lack of trend is not restricted to a specific ecological context or those communities most insulated from human impact.

The lack of trend could be the result of multiple possible scenarios. First, these may be communities resisting perturbations or simply not experiencing significant perturbations. Given the studies in this group come from all possible taxa, realms, climates, and protection statuses, evidence points to communities resisting perturbation, offering some hope that there are areas of the globe where communities are fairing well for now. Alternatively, these may be communities that have experienced or continue to experience significant stress, but lost species or functional diversity outside the observation window. This could be true particularly for North American mammal communities where trophic downgrading and megafaunal losses occurred hundreds of years ago [citation]. Third, these communities may be experiencing directional shifts undetectable by available data. For example, species-level trait data does not capture intraspecific shifts in the trait space, which can represent significant changes in overall functional composition and impact maintenance of ecological processes [citation].

Three of the groups fit under the broad umbrella of changes in redundancy. By definition, if a community gains or loses species while functional metrics are unchanged, those species represent an increase or decrease in redundancy, so we include communities exhibiting gains or losses in species richness with no change in functional metrics or turnover and richness loss with significant turnover in this umbrella. For communities exhibiting loss of redundancy (declining species richness), ecological processes are likely being maintained, but capacity to respond to future stressors is reduced (55). These communities are actually fairing better than expected looking at species-based metrics alone, but are also in a precarious position for maintaining ecological function into the future (56). Conversely, communities exhibiting a increase in redundancy (via an increase in species richness) are becoming better positioned to respond to future stressors, but are not actually expanding their functional capacity as may be assumed by looking at species gains alone (57).

The next group of studies exhibit an increase in species richness and functional richness with significant turnover. While these communities are losing some species that are functionally redundant or functional analogs of species additions, they are gaining even more species that expand the functional space. These communities have a hopeful trajectory, as they are improving their functional capacity and potentially their functional redundancy, likely leading to robust future ecological function. Notably, the studies that exhibited species richness increases (in this group with increasing functional richness, as well as communities without functional richness increases) were exclusively from terrestrial, temperate (sometimes temperate/polar) bird communities and occurred in countries where there has been a significant investment in conservation over the

299 last few decades (United States, Canada, Sweden). Our results are consistent with other functional work in
300 these regions, showing increases in species richness and functional diversity for North American breeding
301 birds over the last few decades after a period of decline(58), and loss of common, functionally general species
302 even as rare species are increasing in North America and Europe (59–61).

303 The final group exhibits decreasing functional evenness. The empirical link between changes in evenness and
304 ecosystem process is the most poorly studied of the metrics, however theory indicates that increased evenness
305 improves function and stability (62). If one or a few species become largely dominant in a community,
306 function will be the result of only those species rather than spread out across a wealth of species responding
307 independently to environmental change (42, 63). Further, there is some evidence that maintaining evenness
308 is important for supporting multifunctionality in communities (64). These communities are therefore of
309 particular concern, especially considering evidence evenness is more sensitive to environmental change that
310 richness (62).

311 While the majority of studies fell into one of the groups discussed in detail above, 25% of the studies
312 exhibited some different combination of change in metrics, underlining the vast heterogeneity of realized
313 change scenarios. We have an indication of the ecological characteristics most likely to lead to some of the
314 change types (e.g. temperate bird communities are gaining species and functional richness), but most types
315 of change are exhibited across many different kinds of communities. Identifying key factors mediating the
316 kind of biodiversity change a community experiences is critical for identifying areas of conservation concern
317 and extrapolating results to areas where functional trait data may not be available. While it is tempting to
318 draw a one to one line between the degree of human impact and loss of functional integrity (in the form of
319 functional redundancy and richness), that relationship is not borne out by our rough metric of human impact
320 or previous taxa-specific or single community work, which is largely mixed (26, 65–67).

4.0.3 Areas of incongruence

322 The addition of functional trait illuminated a few other key areas where a synthesis approach is incongruous
323 with system-specific studies or expectations based on anthropegenic impacts. For example, mean body size is
324 predicted to decrease as a result of climate change impacts and megafaunal loss (68), a phenomenon which
325 has already been well documented empirically and experimentally in multiple taxa (69–72). However, we
326 found no evidence of a trend in *CWM* body size, with the exception of a single study of marine mammals in
327 the Bahamas which showed a significant increase. While the lack of trend could be explained at least in part
328 by data limitations such as shortened observation windows or missing intraspecific data, the fact that only
329 one of the 41 studies for which study-level models were fit showed a change in mean body size, and in the
330 opposite direction of the expectation, is suprising and warrants further reconciliation.

331 Results for protected areas were also surprising given

- 332 changes in diet
- 333 turnover outside protected areas, not inside (though might be driven by the fact that there's generally
  334 less turnover in terrestrial and temperate studies) (37)

4.1 Policy Implications

336 While we found no over all trends in functional metrics, our results should not be interpreted as an indication
337 that the ongoing biodiversity crisis is less severe than previously described, or that there is no concern for
338 functional change as a result of anthropogenic impact. In fact, study-level trends indicate quite the opposite,
339 that functional shifts with unknown implications for ecosystem processes may be going undetected by common
340 species-based approaches, particularly for short observation time windows. While the majority of studies
341 in our dataset did not experience a significant functional loss, a substantial body of work links functional
342 degradation to species losses as a result of direct human intervention in the form of land use change and
343 intensification or habitat fragmentation, indicating that those studies are simply not representative of the
344 kinds of impacts of greatest policy concern (67).

4.2 Future Work

346 We present here four prevailing scenarios of change experienced in bird and mammal communities. While
347 we offer a first discussion of which kinds of change are most common and why, assessing the true global
348 prevalence will require continued efforts to fill data gaps, a well recognized challenge in ecology (6, 12, 73).
349 Still, a "scenarios of change" framework can provide structure for future work addressing functional shifts,

particularly as we reconcile results from broad-scale syntheses with in-depth single system studies. It will be particularly critical to link forms of change to individual drivers to assess which drivers may impact species and functional diversity differently. Understanding those links will help identify where directly measuring functional structure instead of just species change is necessary for understand impacts on a given system. In addition, direct links to drivers will improve our ability to distinguish between communities experiencing no change due to a lack of perturbation from communities with high resilience in the face of disturbance.

Here we identify trends that are statistically significant, however they may not necessarily be ecologically significant. While it is common to link changes in functional metrics to changes in ecosystem processes, those changes are less frequently discussed in terms of the size necessary for ecological impact. The degree of change in a process considered ecological meaningful is somewhat subjective and a function of the system and management context, making identifying the ecological meaning of broad-scale aggregate shifts even more challenging. It is further hampered by the use of species-level trait data, as the traits most closely linked to a process of interest may not be available (74). Future trait collection that explicitly considers existing frameworks for linking traits to processes (e.g. the response and effect framework 15) would facilitate improved ecological interpretation of potential functional changes.

5 Acknowledgments

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